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VARIATION IN THE SPONTANEOUS ACTIVITY OF *PEROMYSCUS*, AS SHOWN BY RECORDING WHEELS

By Lee R. Dice and Sherman A. Hoslett

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INTRODUCTION

Any person who handles considerable numbers of captive *Peromyscus* soon becomes aware of differences in behavior between the several races and species. A prairie deermouse *(Peromyscus maniculatus bairdii)*, for example, appears to be more active and is more likely to jump out of an opened cage than is an individual of the related subspecies *gracilis*.

In an attempt to secure a measure of the differences in spontaneous activity between certain of the races and species of this genus some preliminary experiments with recording wheels were made by F. B. Sumner (1932). After Sumner was forced to give up his studies of *Peromyscus*, the recording wheels which he had used and also certain of his stocks were shipped to the University of Michigan. Here a series of experiments with recording wheels was carried out in the hope of securing dependable measures of the relative activity of a number of species and races.

ACKNOWLEDGMENTS

The Carnegie Institution of Washington furnished the recording wheels used in this study, supplied a number of the stocks of *Peromyscus* which had been collected by F. B. Sumner in California and Alabama, and provided the field expenses for the expedition on which the stock of *Peromyscus truei* was taken. The Museum of Zoology of the University of Michigan provided laboratory space for the study and the salary of the senior author. A grant for the care of the laboratory animals was provided by the Faculty Research Fund of the University of Michigan. Thanks are due J. C. Cross, Paul Hickie, Ralph W. Jackson, and Ruth and Arthur Svihla for collecting certain of the stocks of *Peromyscus* used in the study. The William P. Harris Research Fund helped to support the expeditions on which the stocks of *P. l. texanus* and *P. m. artemisiae* were taken. For suggestions concerning the biometrical treatment of the data we are indebted to Max Woodbury and to C. W. Cotterman. Help with the statistical calculations was given by John A. King and Ruth Osborn. The figure was drawn by Lorraine Ura. The junior author carried out the laboratory study and recorded the data. The senior author has been responsible for the statistical treatments and for the writing of the report.

METHODS OF STUDY

The recording wheels employed in this study were those constructed by Sumner (1932). Each unit consisted of the wheel itself, of a support, and of a recording device. The wheel was constructed of a cylinder of one-quarter-inch mesh galvanized wire cloth eight and one-half inches in diameter and four and five-eights inches wide. One end of this short wire cylinder was closed by a circular piece of three-eighths-inch board, to which one edge of the wire-cloth cylinder was stapled. The axle of the wheel was a bicycle-wheel hub assembly. One end of the axle was bolted to the middle of the circular piece of wood previously mentioned. The hub was supported at its other end by being fastened to a stiff galvanized metal sheet. The wheel, thus supported, turned freely on its ball-bearing axle. The supporting sheet of metal was held in a vertical plane, so that the wheel revolved around a horizontal axis.

A one and one-half-inch hole in the supporting metal sheet, just below the attachment of the hub, allowed the mouse to enter the interior of the wheel. As the mouse inside the drum moved in either direction on the runway formed by the wire-screen cylinder, he caused the wheel to turn. A crank attached to the axle of the wheel operated a mechanical counter, which was fastened to the supporting sheet of metal. This counter recorded the number of turns made by the wheel.

The recording device counted one revolution each time the wheel was turned completely around either clockwise or counterclockwise. It was possible by rocking the wheel backward and forward at a particular point to cause it to record a turn, when in fact only a partial turn had been made. Small back-and-forth movements of the wheel at other points, on the contrary, might be made with no record resulting. The resulting errors are presumed to have balanced each other.

Mechanical difficulties with the wheels or counters developed on a few occasions. The most frequent difficulty was caused by the blocking of a wheel by cotton brought from the nest by the mouse. All daily records which were obviously incomplete due to such difficulties were discarded. This has resulted in a slight variation between the individuals in the number of daily records. It is possible that a wheel may have become temporarily blocked without being detected and thereby may have given too low a record for a certain night. The number of such errors, however, was probably few, and they should not have been cumulative for any particular subspecies.

The wheel cage and its support was placed on top of a regular laboratory cage of the type used for the rearing of *Peromyscus* (Dice, 1929). A large hole was bored in the lid of the cage and from this hole a short, covered tunnel of wire screen led the mouse to the entrance into the wheel. In the cage below the wheel was placed the mouse's nest and also adequate supplies of food and water. The mouse was free to enter the wheel at any time he desired to do so, but the only reward he obtained was the use of the wheel. At any time he wished he could leave the wheel and return again to the more spacious cage below, in which an abundance of food and of water was always available.

A different arrangement was used by Sumner (1932, Fig. 23), who attached a small nest box directly to the support for the wheel. The mouse then was forced to carry out practically all his activity in the wheel. Our observations, however, indicated that where a wheel was available to the mouse he carried out almost all his activities in the wheel and spent very little time in other parts of his cage, except when he was resting in the nest. The advantages of better ventilation and of more space for food and water seemed to justify the use of the larger cage.

All the mice quickly learned to operate the wheels. They seemed actually to enjoy running them, and an individual would often keep his wheel spinning rapidly for minutes at a time. Frequently, an animal would spin the wheel rapidly in one direction for a time and then suddenly stop it, perhaps to start it immediately turning in the opposite direction. The moving parts of each wheel weighed approximately 365 grams. Yet the mice seemed to have no difficulty at all in controlling the motion of the wheels.

Occasionally, a mouse would start a wheel spinning rapidly and then would ride it around and around. The counts of wheel turns obtained while a mouse was "riding the wheel" in this fashion would tend to give an erroneous measure of his activity (see Sumner, 1932:93). While "riding" the mouse was undoubtedly expending less energy than when running inside the wheel. Much energy must have been expended, however, to set the wheel spinning. Further, no record was obtained of the movements of the mouse that failed to turn the wheel, such as his movements in other parts of his cage. Although it is possible that certain mice were more in the habit of "riding the wheel" than others, nevertheless, it is believed that the records of the activities of the animals obtained from the wheels are, in general, comparable.

In the experiments, ten cages, each provided with a wheel of the type described above, were placed side by side on a long laboratory table, all being placed as uniformly as possible in relation to light and heat. One mouse was placed in each cage. Each day the lid of each cage, together with its attached wheel, was shifted to the cage to the right, except that the wheel from the cage on the extreme right end of the line was carried to the extreme left cage of the row. By this procedure each mouse was provided each day with a different wheel. During a period of ten days he used successively all the ten wheels available. Any variation in the ease of turning of the several wheels was thereby equalized.

In order to avoid the periodic variability in activity associated with the estrous cycle of female rodents, only males were used in this experiment. It was impossible to supply individuals of exactly the same age, but all those used were in the prime of life, and no very young nor very old individuals were used in the experiments.

In spite of every effort to select only healthy animals, a few individuals developed evidence of illness and one mouse died before the conclusion of his "tour of duty." The records of any individual which appeared to be ill were discarded, and the animal was replaced by another. It is possible that a few individuals who gave very low records may not have been in the most robust health, but no record was discarded unless the animal was clearly abnormal.

The experiments were conducted over the period from September 14, 1931, to April 10, 1932. The activity of each mouse was measured over a continuous period of fifteen to twenty-seven days. We allowed the mice to be active every day and not just on alternate days, as had been the practice of Sumner. Each mouse of the set of ten under test at one time was usually of a different subspecies or species. The same set of stocks was in general tested together during each month of the series. In a few instances the stocks being tested, however, did not follow this regular order. Two individuals of *sonoriensis* were tested the first month. Only four individuals of *laceianus* were available, and their place was taken in the later months by those of *artemisiae*. Records of only two of *austerus* are available and of only four of *noveboracensis*. In general each mouse was tested only over one period of somewhat less than a month. Five individuals, however, were each tested twice, so that these individuals have contributed more than the others to the means of their stocks.

In the analysis of variance of the records and in the tests of heterogeneity between individuals no distinction is made between repeat series of the same individual and those of separate individuals. In the table of experience according to days in the wheel cages, however, each individual is considered only once.

STOCKS

Individuals of the following mice were used in these experiments:

Peromyscus polionotus polionotus. Seven laboratory-bred descendants of a stock taken by F. B. Sumner (1932, Fig. 15) at Graceville, on the border between Alabama and Florida.

Peromyscus maniculatus artemisiae. Three laboratory-bred descendents of a stock taken by Lee R. Dice, near Pullman, Whitman County, Washington, while on the University of Michigan-Harris Expedition of 1928.

Peromyscus maniculatus austerus. Two field-caught animals taken in 1931 by Arthur and Ruth Svihla near Port Angelus, Clallam County, Washington.

Peromyscus maniculatus bairdii. Five laboratory-bred descendents from a stock taken by Paul Hickie near Lake Village, Newton County, Indiana.

Peromyscus maniculatus sonoriensis. Seven laboratory-bred descendents from a stock taken by F. B. Sumner near San Felipe, Imperial County, California.

Peromyscus leucopus noveboracensis. Four laboratory-bred descendents from a stock taken by Ralph W. Jackson at Cambridge, Dorchester County, Maryland.

Peromyscus leucopus texanus. Six laboratory-bred descendents from a stock taken by Lee R. Dice near Mulato, Tamaulipas, while on an expedition supported in part by the William P. Harris Research Fund.

Peromyscus truei truei. Seven descendents from a stock collected by Lee R. Dice at the Mesa de Maya, Las Animas County, Colorado, while on an expedition supported by the Carnegie Institution of Washington.

Peromyscus pectoralis laceianus. Four field-caught mice taken by J. C. Cross in the vicinity of Austin, Travis County, Texas.

Peromyscus eremicus eremicus. Seven laboratory-bred descendents of a stock taken by F. B. Sumner, in Thousand Palm Canyon, Riverside County, California.

Peromyscus californicus insignis. Seven laboratory-bred descendents of a stock taken by F. B. Sumner, at La Jolla, San Diego County, California.

EFFECTS OF EXPERIENCE ON ACTIVITY

The amount of daily activity of these mice, as recorded by the count of wheel turns, increases with experience for several days. Sumner (1932: 93) noted a "fairly steady increase" in activity from day to day. Such an increase up to the sixth day is clearly demonstrated in our records (Table I). After the sixth day, however, the trend of our records is irregular, and the means for the seventh to twelfth days are less than the mean for the sixth day. The means of only a few of the days after the twelfth and up to the twenty-second day exceed the mean of the sixth day. We fail to verify, consequently, Sumner's statement of a continuous increase in activity. Instead, our records indicate a rapid increase in activity from the first to about the sixth day, after which there is very little further increase in daily activity.

Neither can we verify Sumner's observations that certain mice had to be restrained from overexercising themselves fatally. It is true that one of our mice died during the course of the experiments. Several others were inactive and apparently not in good health. These individuals were removed from the experiments and were replaced by other individuals. We are not convinced, however, that the death of the one individual or the weakened condition of the others were caused by overexercise in the wheels. On the contrary, the most active mice continued to make high records of wheel turns night after night with no evidence of any deterioration in health. Nor can we detect any evidence that a high record for one night was followed by a lower record the following night, such as might result from fatigue.

TABLE I

Activity records of *Peromyscus* according to day of experience with the wheels. Mean daily turns of recording wheels per individual from first to twenty-second days for all stocks and for all test periods. Males only.

Day	Mean Turns Per Individual	Day	Mean Turns Per Individual
1	5,792	14	16,750
2	7,316	15	16,672
3	9,801	16	17,443
4	10,872	17	15,625
5	11,983	18	17,457
6	16,350	19	15,765
7	14,451	20	17,403
8	15,214	21	17,116
9	14,885	22	16,661
10	14,868	Average of all 22 days	14,875
11	15,767	Average of last 19 days only	16,347
12	15,627		
13	19,134		

Activity records for the individual animals are available for periods varying from twenty-two to thirty days, except for one individual of *laceianus*, of which we have records for only eighteen days. In view of the lesser activity of the animals during the first five days of their experience in the wheels compared to their records for the sixth and later days, the most accurate comparisons between individuals and between stocks would have been obtained by throwing out all the records of the first to fifth days. This, however, would have resulted in a considerable loss of information. We have accordingly compromised by omitting from the comparisons within and between individuals and between stocks all records of the first to third days, inclusive, while including all the records from the fourth day onward.

MONTH-TO-MONTH VARIATION IN ACTIVITY

The observations extended over the period from September 11 to April 10 and they therefore covered seven months. It is consequently necessary to examine the records in the search for possible variation in the activity of the animals which might be in any way correlated with the month in which the record was taken. One thinks first of all of a possible relation between temperature and seasonal activity.

The temperature of the laboratory varied somewhat during each day and also from day to day. The fluctuations that occurred, however, were all well within the range that these mice can easily tolerate. At no time was there any extreme fluctuation in laboratory temperature, and the variation from month to month was relatively slight (Table II). Temperature records are not available for the period from February to April, but the Laboratory was maintained in the same manner during the whole period of study, and it may be assumed that the temperature varied during the later months in approximately the same way as during the earlier months of the experiments.

When we examine the activity-wheel records of the mice arranged by months (Table II), we are unable to discover any seasonal or monthly trend. The records of the mice of all the stocks taken together vary somewhat from month to month. A different pattern is exhibited, however, when the monthly records are based on the first twenty-two days of each period rather than when they are based on the records of the fourth to twenty-second day only (Table II). The species and races represented in the experiments varied somewhat from month to month. When an attempt is made to overcome this source of variation by considering only those stocks represented every month, then a still different pattern of the monthly means is obtained.

The variation from month to month in the activity of the mice is irregular, and no indication is exhibited of any trend which can be correlated with progressive seasonal changes in the outdoors. No seasonal change in activity should perhaps be expected in mice kept in the relatively constant environment of the laboratory and always provided with an abundance of water and standard food.

In our further analysis of the activity-wheel records of these mice we have, consequently, paid no attention to the month when each record was made, assuming that season has had no appreciable effect on the activity of the animals.

VARIATION FROM DAY TO DAY IN THE ACTIVITY OF THE SAME INDIVIDUAL

Inspection of the original records demonstrates considerable variation from day to day in the activity of every animal used in the experiments (Table III). A part of this day-to-day variation is due to experience with the wheels, as has been pointed out above. After about the sixth day, however, the day-to-day variations in the records can no longer be certainly ascribed to gain in experience. The records continue, nevertheless, to fluctuate more or less from day to day regardless of how long an animal is under observation in the wheels.

The maximum daily records made by the individuals of the several stocks range from 38,143 turns for *polionotus* to 58,760 turns for *noveboracensis*

TABLE II

Activity records of *Peromyscus* by monthly test periods. Mean daily turns of recording wheels per mouse. Males only. Records for days after the twenty-second not included.

Period	Mean Daily Turns		Number of Mice	Temperature (Degrees F.)			
				Daily Means		Daily Extremes	
	1st–22nd Days	4th–22nd Days		Minimum	Maximum	Minimum	Maximum
Sept. 11–Oct. 2	15,948	17,557	9	73.5	78.2	66	85
Oct. 3–Oct. 29	13,959	15,092	9	70.6	78.2	66	82
Oct. 30–Nov. 20	13,436	15,558	7	69.9	73.2	68	78
Dec. 7–Dec. 30	13,850	16,408	7	70.0	76.7	68	84
Jan. 9–Jan. 30	16,090	17,169	8	69.3	73.3	67	81
Feb. 15–Mar. 8	12,000	13,073	6	...	...	..	..
Mar. 20–Apr. 10	17,474	18,409	9	...	...	..	..

TABLE III

Illustration of day-to-day variation in activity-wheel records of *Peromyscus*. Records of three stocks for the September–October period. Males only.

Date	Number of Turns Per Twenty-four-hour Period		
	polionotus No. 8501	*bairdii* No. 8450	*noveboracensis* No. 8996
Sept. 11	307	2,734	2,831
12	2,240	5,110	2,243
13	1,163	11,209	2,904
14	1,626	8,323	5,526
15	725	8,227	8,541
16	4,953	13,352	12,281
17	2,771	14,926	12,809
18	4,415	12,314	20,126
19	3,839	12,102	20,865
20	4,409	13,523	18,356
21	1,600	12,861	17,906
22	2,280	16,896	17,754
23	1,134	13,820	15,235
24	2,860	21,594	4,222
25	3,817	26,950	6,044
26	3,941	19,906	8,571
27	1,285	27,548	6,639
28	1,875	22,921	5,873
29	1,037	24,737	8,524
30	510	22,593	7,029
Oct. 1	1,564	20,572	5,846
2	1,137	6,226	5,435

(Table IV). The maximum records are in every case, of course, considerably above the mean number of turns per day of the respective individual. The conclusion may be drawn that the individuals were actually capable of a much greater amount of activity than they usually exhibited.

Notwithstanding its day-to-day variability in number of wheel turns, each individual tends to maintain something of a general level of activity. In the analysis of variance of the records (Table V) the day-to-day variability "within individuals" is significantly less than the variability between individuals of the same stock. The comparison of the activity records of the several individuals used in the experiments is indicated, therefore, to be justified.

VARIATION IN ACTIVITY BETWEEN INDIVIDUALS OF THE SAME STOCK

The individuals of the same stock, unfortunately, often differ greatly from one another in their records in the wheels. As was pointed out in the previous

TABLE IV

Records of spontaneous activity of certain species and subspecies of *Peromyscus*. Recording-wheel turns per twenty-four-hour period. Males only. Records of first three days for each mouse omitted.

Peromyscus Stock	Indi-viduals Tested	Daily Records	Mean	Individual Means		Individual Extremes	
				Minimum	Maximum	Minimum	Maximum
polionotus							
polionotus	7	157	5,815	2,259	21,917	124	38,143
maniculatus							
artemisiae	3	64	16,594	14,474	19,880	93	39,961
austerus	2	68	30,676	23,000	34,864	4	50,919
bairdii	5	159	25,881	16,895	27,917	11	49,912
sonoriensis	7	176	22,636	8,333	39,526	810	53,788
leucopus							
noveboracensis	4	108	19,648	7,632	31,815	706	58,760
texanus	6	140	14,829	4,250	24,333	204	44,588
truei							
truei	7	157	14,146	2,778	28,143	197	43,725
pectoralis							
laceianus	4	85	14,953	2,167	39,000	2,156	53,125
eremicus							
eremicus	7	159	16,459	6,120	25,632	1,295	53,767
californicus							
insignis	7	157	16,484	3,105	26,182	110	49,480
All stocks	59	1,430	17,520.9	2,167	39,526	4	58,760

TABLE V

Analysis of variance of activity of *Peromyscus* in recording wheels. Thousands of turns per day. Records for first three days for each mouse omitted.

Source of Variation	*D.F.*	Sum of Squares	Mean Square	*F*
A Within individuals (between days)	1,371	82,743.2	60.35	B/A 33.70*
B Between individuals (within stocks)	48	97,623.7	2,033.83	C/B 2.62†
C Between stocks	10	53,253.0	5,325.30	
Total	1,429	233,619.9		

* Significant at the 1 per cent level.
† Significant at the 5 per cent level.

section, the differences in activity between individuals is significantly greater (at the 1 per cent level) than the day-to-day differences within individuals (Table V).

An illustration of the amount of the difference in activity between individuals is given by the *laceianus* stock, which consisted of four animals. Two of these animals were relatively inactive and neither ever exceeded 16,000 wheel turns in any twenty-four-hour period during the whole course of the experiments. In fact, the maximum number of turns made by one of these animals in any twenty-four-hour period was only 3,461. The third individual, on the contrary, was very active, so much so that he never ran less than 20,000 turns per night, and on only two nights did he make less than 32,000 turns of the wheel. The fourth mouse was variable in his activity and ran 24,000 turns or more on each of five nights, but less than 16,000 turns on ten other nights.

The heterogeneity between the activity records of the several individual mice tested in each stock has been calculated by the method described by Snedecor (1946: 206). We compared the number of days on which each mouse made 16,000 turns or more with the number of days on which he made less than 16,000 turns of the wheel. The chi-squares obtained indicate a highly significant departure from homogeneity for every stock except for the *austerus* stock, which consisted of only two individuals (Table VI). In every other stock certain of the individuals ran over 16,000 turns per night for a majority of the nights, while other individuals in the same stocks failed to make as many as 16,000 turns on most of the nights. In *polionotus*, for example, out of seven individuals tested, four made no daily record as high as 16,000 turns, two mice exceeded 16,000 turns on only one night each, while one mouse made over 16,000 turns on eighteen out of twenty-four nights.

TABLE VI

Heterogeneity of activity-wheel records between individuals of the same stock of *Peromyscus,* calculated from the proportion of days on which each individual made records of 16,000 turns or more. Records for first three days for each mouse omitted.

Stock	Proportion of Days Above 16,000 Turns	Degrees of Freedom	Heterogeneity Between Individuals Chi-square
polionotus			
polionotus	.13	6	99.320
maniculatus			
artemisiae	.47	2	95.904
austerus	.84	2	.356
bairdii	.78	6	51.556
sonoriensis	.57	7	101.421
leucopus			
noveboracensis	.60	4	60.664
texanus	.44	5	50.331
truei			
truei	.40	6	69.847
pectoralis			
laceianus	.28	3	68.520
eremicus			
eremicus	.45	6	68.952
californicus			
insignis	.53	6	94.039

COMPARISON OF THE DAILY ACTIVITY OF THE SEVERAL RACES AND SPECIES

The high degree of heterogeneity between the activity records of individual mice within the same stock, demonstrated in the preceding section, makes any comparison of the stocks open to suspicion. Nevertheless, it seems worth while to attempt such a comparison. The conclusions reached will only be true for the individuals tested. If other individuals had been used as representatives of a particular stock that stock mean might have been considerably different from the mean here used as a basis for comparison.

That the activity records differ significantly between the stocks is shown by the analysis of variance (Table V). The mean square between stocks is high and indicates that this source of variation is very important. In fact, the "between stocks" variation is significantly higher than the "within stocks" variation, the F value of the difference being close to the 1 per cent level of probability.

In order to test the significance of the differences in spontaneous activity exhibited by the mice of the several stocks we have used a procedure suggested by Max Woodbury. The number of days on which the records of all the individuals of each stock exceeded 16,000 was counted and also the number of days on which the number of turns was less than 16,000. The comparison of the activity of any two stocks could then be made by the calculation of chi-square from a 2 by 2 table. The method is illustrated in Table VII. Some loss of efficiency results from the use of this method, but it is sufficiently discriminatory for our purpose.

TABLE VII

Example of comparison of twenty-four-hour activity-wheel records of two stocks of *Peromyscus maniculatus* by means of a 2 by 2 table. Records for first three days for each mouse omitted.

Turns Per Day	*bairdii*	*sonoriensis*	Totals
Number of days with turns of 16,000 or over	124	100	224
Number of days with turns under 16,000	35	76	111
Total	159	176	335

Chi-square=16.896, with 1 degree of freedom.

The mean of the daily activity-wheel records of the *polionotus* mice is considerably lower than the mean of any other of our stocks (Table IV and Fig. 1). The difference in means between the *polionotus* stock and that of any other stock, as measured by chi-square, is highly significant (Table VIII). Attention should, however, be given to the high mean record, 21,917 turns per night, of one individual of *polionotus*. We cannot conclude, therefore, that *polionotus* in general is less active than are the other species and races. The failure of most of the *polionotus* individuals to make good records may perhaps have been due to a failure to learn how to use the wheels. These mice, moreover, are considerably lighter in weight than are the mice of any of the other stocks, and it is possible that most of them found it difficult to operate the wheels.

Austerus has the highest mean for daily activity-wheel turns of all the stocks. Its mean significantly exceeds the means of all the other stocks except *bairdii*. We are not disposed, however, to place very great dependence on this high mean, because only two individual mice were tested.

The *bairdii* stock falls next below *austerus* in mean daily number of wheel turns. The difference between the *bairdii* mean and the mean of every other stock, except *austerus*, is highly significant (Table VIII). In spite of the heterogeneity of the records we believe that this high mean for *bairdii* may actually indicate a real difference from the other stocks in activity. In the laboratory the mice of the subspecies *bairdii* are noticeably more nervous and more active than are most other kinds of *Peromyscus*.

TABLE VIII

Chi-square values derived from comparison of several stocks of *Peromyscus* according to proportion of activity-wheel turns above and below 16,000 per day, respectively. 1 degree of freedom. Records for first three days for each mouse omitted.

Stock	*truei*	*texanus*	*laceianus*	*eremicus*	*insignis*	*artemisiae*	*noveboracensis*	*sonoriensis*	*bairdii*	*austerus*
polionotus	30.281	35.470	8.901	40.541	57.344	30.265	67.183	69.946	135.592	106.510
truei	......	.361	3.387	.858	5.121	.849	10.832	9.251	46.872	36.400
texanus	......	......	5.292	.088	2.560	.194	7.160	5.475	37.380	30.210
laceianus	......	......	.....	6.745	13.564	5.490	14.129	18.778	57.374	46.856
eremicus	......	......	.....	......	1.818	.047	6.124	4.449	35.960	28.837
insignis	......	......	.....	......	......	.653	1.609	.523	22.063	19.228
artemisiae	......	......	.....	......	......	......	3.121	1.869	20.672	20.032
noveboracensis	......	......	.....	......	......	......	......	.423	9.242	10.580
sonoriensis	......	......	.....	......	......	......	......	......	16.896	14.867
bairdii	......	......	.....	......	......	......	......	......	....	1.004
austerus	......	......	.....	......	......	......	......	......	....	....

The remaining stocks, *sonoriensis* to *truei* (Fig. 1), exhibit considerable differences in their stock means of number of wheel turns per day. The individual means, however, overlap broadly between these stocks. Furthermore, many of the differences between the stock means are not significant. We consequently prefer not to attempt to draw any conclusions about possible differences in spontaneous activity between these stocks.

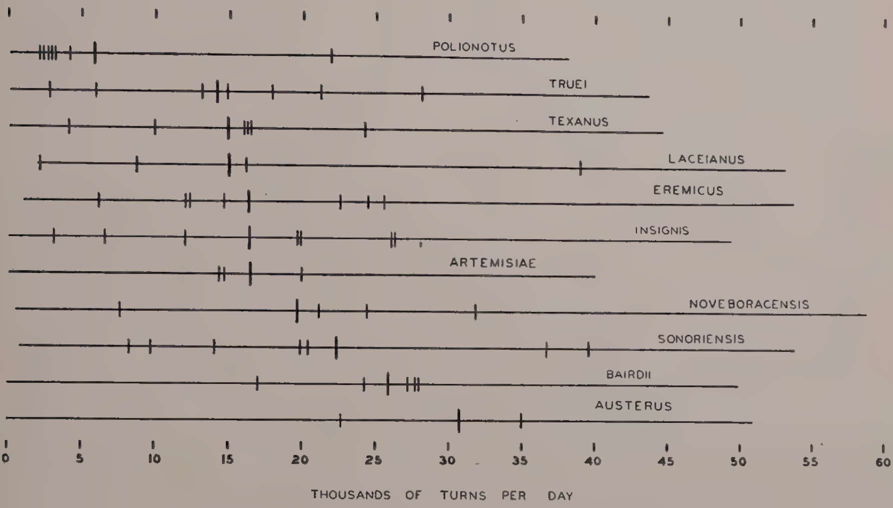

FIG. 1. Graphic comparison of daily activity-wheel records of several races and species of *Peromyscus*. Records for first three days for each individual are omitted. The long line represents for each stock the minimum and maximum number of daily turns for any individual. The heavy crossbar indicates the mean number of daily turns for the stock. The lighter crossbars indicate the means of the individuals.

The general indications from these comparisons are that the mice of the subspecies *bairdii* exhibit a greater amount of spontaneous activity than do the mice of the several other races and species of *Peromyscus* tested, with the possible exception of *austerus*. The species *polionotus* made a relatively low record on the wheels, but this low record may have been due to the relatively small size of these mice. The heterogeneity of the records of the individual animals within the stocks makes it impossible to draw any positive conclusions.

VALUE OF RECORDING WHEELS FOR THE MEASURE OF MAMMALIAN ACTIVITY

As a result of our experience with these recording wheels we are of the opinion that they give an unsatisfactory measure of spontaneous activity for mice of the genus *Peromyscus*. The chief difficulty lies in the great variation in the activity-wheel records between individuals of the same stock. Any satisfactory comparison between stocks should, therefore, be based on the records of many individuals. Because of the effect of experience on the number of turns of the wheel made per night, however, the records of the individuals only become of most value after a period of training of five or more days. The securing of records from any large number of individuals is consequently laborious and time consuming.

Some of the variability in the average daily number of wheel turns made by the individuals within the stocks may have been correlated with differences in the weights or strengths of the individuals. We did not weigh our animals, and consequently we cannot test this possibility. It seems possible, for example, that the individuals of small size, such as those of the species *polionotus,* may have been considerably handicapped in turning the wheels, as compared to the individuals of larger and heavier species. It should be pointed out, on the other hand, that the stock *insignis,* in which the individuals are the largest among those here tested, was less active on the wheels than the smaller form *bairdii.* There is then no regular increase in number of wheel turns per day correlated with increase in body size. Nevertheless the possibility remains that the low records of most of the *polionotus* may be due to their small body weight compared to the weight of the wheel.

Activity wheels are undoubtedly of value for certain psychologic or physiologic studies in which the same individual can be tested under varying conditions. For the comparison of the spontaneous activity of races and species, however, these wheels are not fully satisfactory.

These recording wheels, nevertheless, have demonstrated that the mice of the genus *Peromyscus* are able to perform prodigious feats of activity. The individuals weigh from about twelve (for *polionotus*) to about sixty (for *insignis*) grams, but all of them are able almost instantly and with seeming ease to start an activity wheel to spinning rapidly or to decelerate and to stop very quickly a rapidly turning wheel. Since the moving parts of the wheel weigh approximately 365 grams, the amount of energy required to overcome its inertia, either when at rest or when in motion, must for a small animal be considerable.

A second requirement for energy in connection with the operation of these recording wheels is to overcome the friction of the wheel bearings and of the air. Although the wheels turn on ball bearings, the friction loss during an average night's activity must be considerable.

A third source of energy loss for an animal turning an activity wheel is that consumed by his running movements. It requires a considerable amount of energy for any animal to run on a level surface. In turning a wheel the animal actually is running all the time up a slight incline.

When we translate the number of turns of the wheel into equivalent distances traveled by the animals, our estimates are surprisingly high. The average number of turns per day for all the mice (not counting the first three days of experience for each one) was 17,521. Two individuals each averaged 39,000 turns or more per day for a whole period of nineteen or more days. The highest record made in a single twenty-four-hour period by any mouse (of the subspecies *noveboracensis*) was 58,760, but a number of other individuals belonging to several races and species each made records of over 50,000 turns in one day. We have no estimate of the proportion of turns during which each animal "rode" the wheel. It is our impression that most of the animals actually ran during most of the time when the wheels were turning. In our estimates of the distances run by the mice, we shall, therefore, consider that the mice actually ran the whole number of turns per day recorded by the wheels.

If we consider the race track of the animal on the inside of the circumference of the eight and one-half-inch wheel to be two feet, and if we accordingly treat 2,500 turns of the wheel as approximately equal to one mile of travel by the mouse, then the equivalent running distance per mouse of all those tested would average about seven miles per day. Many of the individuals averaged an equivalent of more than twelve miles per day for periods of nineteen days or more. A number of individuals actually ran the equivalent of twenty miles or more within a twenty-four hour period. The maximum number of turns by any individual in one day is equivalent to about twenty-three miles of travel.

We have no measures of the actual energy output of these small mammals, but when we consider the amount of energy needed to overcome the inertia of the recording wheels, the amounts absorbed by friction in the wheel bearings and by the air resistance, and the amount required by the mice for their running, we can assume that the energy output by each individual animal per day compared to its weight must be very high.

SUMMARY

The number of turns of recording activity wheels made per twenty-four-hour period by adult males of seven species and of four additional subspecies of *Peromyscus,* increases from the first up to the sixth day of experience. After the sixth day there is little further increase in daily activity.

No evidence was secured for any seasonal change in spontaneous activity over the period from September to April.

Each individual exhibits considerable variation in his day-to-day record of activity, but the amount of variation "within individuals" is significantly less than that "between individuals."

Individuals of the same stock vary greatly in the mean number of wheel turns made per twenty-four-hour period. This heterogeneity makes unreliable any comparison of the activity of the several species and subspecies based on recording-wheel records.

The species *polionotus* exhibited the lowest mean daily number of wheel turns of all our stocks, but this low mean may have been due to the light weight

of the animals compared to the weight of the wheels or to other causes, and does not necessarily prove spontaneous activity was less for these than for the other forms.

The subspecies *bairdii* had a significantly higher mean number of daily turns than did any other stock except *austerus,* which was represented by only two individuals. The high mean of *bairdii* may possibly represent a higher rate of spontaneous activity than was attained by the other races and species tested, because individuals of *bairdii* in the laboratory are noticeably more nervous and more active than are most other forms.

Recording activity wheels are not fully satisfactory for the measure of spontaneous activity in small mammals. They nevertheless have demonstrated that the mice of the genus *Peromyscus* are very energetic. The average number of turns per mouse per twenty-four-hour period after the third day of experience in the wheels was 17,521. Two individuals each averaged 39,000 or more turns per day over periods of nineteen or more days. A number of individuals belonging to several different races and species each made over 50,000 turns of the wheel in a single day.

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Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price, $.30.